

## Spatial and temporal patterns of ground vegetation dominants in mountain spruce forests damaged by sulphur air pollution (Giant Mountains, Czech Republic)

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We studied ground vegetation dynamics during the decline and recovery of mountain Norway spruce forests damaged by SO<sub>2</sub> air pollution and associated stress factors. Changes in areal extent of the ground vegetation dominants, moss layer and spruce litter and trajectories of these changes, recorded at a spatial resolution of 5 × 5 cm, were analysed in 1-m<sup>2</sup> squares located in plots differing in dynamics of spruce canopy cover. Spruce litter patches diminished during spruce stand decline being colonised by *Avenella flexuosa*, *Calamagrostis villosa* (in canopy gaps) and *Vaccinium myrtillus* (under gradually defoliating tree crowns). After several years of spatially dynamic coexistence of the grasses, *C. villosa* began to retreat being replaced by *A. flexuosa*. *Vaccinium myrtillus* then re-entered these grass stands. In less affected spruce stands, the dominants partially retreated without competing with other ground vegetation. Moreover, the applied GIS spatio-temporal analysis revealed substantial spatial movements of the dominants over the plots.

### Introduction

The synergistic effect of high and long-lasting air pollution (especially SO<sub>2</sub>), accompanied by deposition of acidifying compounds (resulting in a decrease in soil pH, leaching of basic cations and subsequent aluminium toxicity in podzol soils), climatic stress (climatic extremes in March 1977 and January 1979 (Vacek and Matějka 1999) and an infestation of weakened forests by the spruce bark beetle (Vacek and Matějka 2010), led to an extensive decline and dieback of Norway spruce forest ecosystems in the Giant Mountains (Mts.) (Czech Republic) in the 1970s and 1980s (Kooijman *et al.* 2000, Hruška and Cienciala 2003,

Vacek *et al.* 2013). Power stations and other heavy industries burning brown coal with high sulphur content were primary sources of this pollution. Between 1980 (the beginning of measurements) and 1991, mean annual concentration of SO<sub>2</sub> fluctuated between 10 and 35 µg m<sup>-3</sup> per year (Vacek *et al.* 2013). The highest maximum daily concentration of SO<sub>2</sub> (140 µg m<sup>-3</sup>) was measured at the Labská bouda Station located in the centre of the Giant Mts. (Vacek and Lepš 1996). Health status monitoring of forest stands, carried out in the Giant Mts. since 1979, has confirmed the principal role of air pollutants in forest dieback; the northwestern parts of the mountain range were the most threatened (Vacek *et al.* 2013).

Due to the large-scale decline of coniferous forests caused by the above-mentioned stress factors, a total forest area of 7000 ha was felled in the Giant Mts. (Vacek and Matějka 1999). Surviving trees showed marked loss of needles (Polák *et al.* 2007), reduced radial increment (Sander *et al.* 1995), suppressed fructification and viability of seeds (Vacek 1981), retreat of ectomycorrhizal basidiomycetes (Cudlín and Chmelíková 1996) and large-scale infestation by insects (Grodzki *et al.* 2004). The decline of spruce stands was accompanied by changes in floristic composition and in abundance of ground vegetation. Expansion of patches of grasses and nitrophilous species was particularly noteworthy (Soukupová and Rauch 1999, Vacek and Matějka 1999). The shift in ground vegetation towards grass species may result in further changes in soil conditions, through the whole soil profile (Bonifacio *et al.* 2008). Changes in the forest understory can also potentially affect spruce seedling recruitment and thereby alter the internal dynamics of these forests (Vacek *et al.* 1999). Grass stands were found to provide less favourable conditions for seedling emergence and survival than other microhabitats such as litter patches, mosses or *Vaccinium myrtillus* vegetation, which occur more in undamaged forest ecosystems (Vávrová *et al.* 2007).

Successional trends in ground vegetation following the dieback of the mountain Norway spruce forests caused by SO<sub>2</sub> air pollution differed depending on site moisture. At moist sites, four phases of ground vegetation succession could be distinguished: (i) a gradual retreat of bilberry (*Vaccinium myrtillus*), the dominant species in forests and young clearings; (ii) expansion of hairy reed grass (*Calamagrostis villosa*) in clearings of 4–6 years old; (iii) gradual decline of this grass accompanied by expansion of wavy hair grass (*Avenella flexuosa*), and (iv) partial retreat of *A. flexuosa* after several years. At dry sites, *A. flexuosa* usually colonised clearings directly after the decline of *V. myrtillus* and reached dominance earlier (van Ron 1993).

The dynamics of *C. villosa* and *A. flexuosa* in partially damaged stands showed analogous shifts in abundance after intensive defoliation, as shown for clearings (Pyšek 1992, Soukupová 1996). Environmental conditions under healthy

forest canopy favoured *A. flexuosa* as a shade-tolerant species requiring smaller amounts of nutrients than *C. villosa*. At sites where intensive defoliation had occurred, *A. flexuosa* stands were invaded by *C. villosa* (Pyšek 1992, Soukupová *et al.* 1995). The dominance of *C. villosa* lasted seven or eight years only. After this time, *C. villosa* was limited by low organic matter content and *A. flexuosa* subsequently recurred among its senescent tillers and finally *C. villosa* was mostly replaced by *A. flexuosa* (Soukupová *et al.* 1998).

In the first half of the 1990s, air pollution began to decrease in the Giant Mts. region as a consequence of desulphurisation of power stations and of other actions by heavy industry aimed at minimising environmental impacts. The first important reduction of sulphur deposition, from 50–80 kg ha<sup>-1</sup> year<sup>-1</sup> to 26–36 kg ha<sup>-1</sup> year<sup>-1</sup>, occurred between 1994 and 1996. A second and less pronounced reduction, from 30–35 kg ha<sup>-1</sup> year<sup>-1</sup> to 6–10 kg ha<sup>-1</sup> year<sup>-1</sup>, occurred between 1998 and 2000 (Vacek *et al.* 2013). The reduction of air pollution has resulted in interruption of the large-scale decline and dieback of spruce stands and has allowed partial regeneration of surviving trees (Vacek *et al.* 2007). Changes in ground vegetation accompanying the decline of spruce stands proceeded in many localities until the end of the 20th century. Thereafter ground vegetation probably responded to the interruption of tree mortality and to the resulting stabilisation of light conditions within the stands. The previous expansion of ground vegetation stopped, the dominant grasses *C. villosa* and *A. flexuosa* began to retreat and the remarkable increase in cover of mosses occurred (Vávrová *et al.* 2009).

The objective of this paper is to better explain the complex ground vegetation dynamics occurring in mountain Norway spruce forests damaged by the synergistic effects of high and long-lasting air pollution and other accompanying stress factors. This study was performed as part of a long-term observation of permanent research plots chosen at the beginning of the 1990s (after considerable reduction of SO<sub>2</sub> air pollution) to represent different stages of forest decline (from slightly damaged to nearly dead spruce stands) resulting from different levels of air pollution stress in the past. Since that time,

the development of mountain Norway spruce ecosystems has been studied in the Giant Mts. (Vacek and Lepš 1996, Vacek and Matějka 1999, Vávrová *et al.* 2009, Vacek *et al.*, 2013). In this paper, we (i) assess the fine-scale dynamics of ground vegetation within the damaged spruce stands including its spatial extent; (ii) track the transition trajectories of ground vegetation dynamics, especially colonisation of spruce litter patches and consecutive replacement of the dominants; and (iii) determine the relationship between these transition trajectories and canopy cover at the beginning of the observations and its subsequent development on individual plots. We compare the changes in ground vegetation among the plots differing in dynamics of spruce stand and in time since canopy opening and we try to deduce and reconstruct successive patterns of ground vegetation dynamics during and after the period of forest decline. We formulate two hypotheses: (i) in addition to changes in cover values of ground vegetation components detectable at the level of spruce stands, a considerable part of the dynamics in ground vegetation occurs at the microhabitats scale and results in changes in location of ground vegetation dominants within the spruce stands; and (ii) the fine-scale dynamics in ground vegetation and its transition trajectories differ among mountain Norway spruce forests with different crown damage and stress-response history.

## Methods

### Study area and sampling design

The study was carried out in the Giant Mts. (Krkonoše in Czech) situated on the Czech-Polish border in central Europe. Plots were located in autochthonous climax Norway spruce (*Picea abies*) stands from the upper mountain forest zone. The altitude ranged from 1192 m a.s.l. to 1317 m a.s.l. The bedrock in the study region consists of acidic metamorphic rocks (mica schists, phyllites, ortho-gneisses) and granite. The climate is cold-temperate with prevailing westerly winds. Average annual precipitation varies with altitude and aspect from 857 mm to 1260 mm, and the mean annual temperature

decreases with altitude from 6.1 °C to 2.6 °C (Fanta 1969).

Five study plots, 50 × 50 m in size, were established on a NW–NE transect through the Giant Mts. in the first half of the 1990s, after the considerable reduction of SO<sub>2</sub> air pollution, which occurred soon after the political changes of 1989–1990. The plots were chosen to represent different stages of forest decline caused by different levels of past air pollution stress (Table 1). At the Mumlavská hora and Alžbětinka plots located in the western part of the Giant Mts., a massive decline had already occurred by the 1980s (Vacek *et al.* 2013). The spruce stands of the Modrý důl and Slunečné údolí plots were less damaged. They exhibited a relatively dense canopy cover and a low percentage of dead trees in the first observation time in 1995. Their subsequent tree layer dynamics differed, however. Canopy cover decreased considerably in the Slunečné údolí plot, while the corresponding decrease in Modrý důl was relatively moderate. The Pašerácký chodníček plot differed from the other plots by its denser spruce stand and its clustered horizontal structure. Large canopy gaps were due to the location of the stand near timberline, with hardly any influence of forestry management. In regard to the great variability of site conditions in the Giant Mts., the plots varied in altitude (from 1185 to 1317 m a.s.l.), aspect, slope, prevailing soil type and stand age. Short-listed plot characteristics relative to the spruce stand initial stage of decline and its subsequent dynamics are shown in Table 1. Canopy cover of the spruce stand was assessed as a ratio of areal extent of all crown projections to the total plot area. For other characteristics see Vávrová *et al.* (2009).

Norway spruce (*Picea abies*) was the sole member of the tree layer in all stands investigated. The ground vegetation was dominated by *A. flexuosa*, *C. villosa* and *V. myrtillus*. For a complete list of ground vegetation species occurring at each of the study plots see Soukupová and Rauch (1999). Nomenclature used in this study follows Kubát (2002).

Each plot was divided into 25 blocks in 5 × 5 arrangements, 10 × 10 m in size. Four 1 × 1 m squares were randomly selected, laid out and marked by wooden or plastic sticks in each

block, i.e., 100 squares in each plot (except for the Mumlavská hora plot, where only 60 squares in 15 blocks were established and examined). Regarding the negligible number of Norway spruce seedlings on this plot the 60 squares are a representative number. Vegetation of the 1-m<sup>2</sup> squares was analysed three times: in 1995, 2002 and 2006. Vegetation maps were drawn manually using a wooden frame with a 10 cm rectangular grid and the objects were mapped if covering at least 5 × 5 cm. All herb layer species present in the plots and other ground cover, such as spruce litter, decaying wood, branches, stones and stumps, were mapped. For the dominant species (*A. flexuosa*, *C. villosa*, *V. myrtillus*), two levels of stand density (sparse or dense) were distinguished. If the dominant species covered more than 50% of the 5 × 5 cm, or a bigger area, the stand was rated as dense; if it covered less than 50%, the stand was rated as sparse. Moss layer species were not distinguished and were recorded as one category called “mosses”.

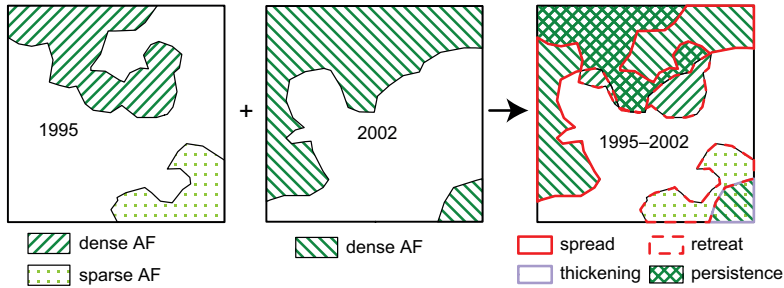
# Data processing

The vegetation maps of 1-m<sup>2</sup> plots were digitised using ArcGIS ver. 9.1 (Esri Inc., Redlands, CA, US) to create the following GIS (Geographic Information System) vector layers for each year: *A. flexuosa*, *C. villosa*, *V. myrtillus*, other herbaceous vegetation and a mixed layer encompassing mosses, spruce litter patches and other ground cover (decaying wood, stones, stumps, tree stems, roots etc.). For the purposes of this article, ten basic ground cover categories were distinguished: sparse stand of *A. flexuosa*, dense stand of *A. flexuosa*, sparse stand of *C. villosa*, dense stand of *C. villosa*, sparse stand of *V. myrtillus*, dense stand of *V. myrtillus*, mosses, spruce litter, other herbaceous vegetation and other ground cover. Spatial analysis of the ground vegetation dynamics was performed in two subsequent study periods, 1995–2002 and 2002–2006.

In order to analyse ground vegetation dynamics, we first calculated areas of polygons belong-

**Table 1.** Characteristics of the study plots, emphasising the initial stage of spruce stand decline and subsequent dynamics. The plots are arranged in order of increasing damage to spruce stand by air pollution. For other characteristics see Vávrová *et al.* (2009) and Soukupová and Rauch (1999). Names of plant communities at individual plots were taken from Soukupová and Rauch (1999). The interpolated average daily temperature values and average of daily rainfall amount come from years 1960 to 2012.

Plots	Modrý důl	Slunečné údolí	Pašerácký chodníček	Alžbětinka	Mumlavská hora
Latitude	50°43'13''N	50°44'26''N	50°44'25''N	50°45'34''N	50°47'56''N
Longitude	15°42'25''E	15°45'29''E	15°45'56''E	15°31'15''E	15°27'53''E
Altitude (m)	1237	1241	1317	1192	1185
Aspect	S	SW	SW	NW	SW
Slope	22°	31°	18°	14°	5°
Prevailing soil types	Podzol, Leptosol	Podzol	Podzol, Leptosol	Leptosol, Histosol, Podzol	Podzol
Temperature (°C)	2.8	2.7	2.8	3.0	3.4
Precipitation (mm)	1346.3	1312.5	1311.3	1377.7	1363.2
Stand age (1997)	121	154	145	200	200
Number of live trees in					
1992	98	88	145	65	12
2000	94	77	132	61	3
2008	93	74	124	59	3
Canopy cover (%) in					
1996	0.65	0.60	0.50	0.35	0.05
2000	0.54	0.36	0.32	0.29	0.02
Vegetation community type	<i>Calamagrostio villosae-Piceetum fagetosum</i>	<i>Calamagrostio villosae-Piceetum typicum</i>	<i>Calamagrostio villosae-Piceetum typicum</i> var. <i>avenellosum</i>	<i>Athyrio alpestris-Piceetum typicum</i>	<i>Sphagno-Piceetum molinietosum</i>



**Fig. 1.** A scheme illustrating the creation of polygons for a particular dominant (AF: *Avenella flexuosa*). The polygons display spread, retreat, and/or changes from a sparse to a dense (thickening) or from a dense to a sparse (thinning) stand during the period under consideration (1995–2002). The figure represents a 1-m<sup>2</sup> plot.

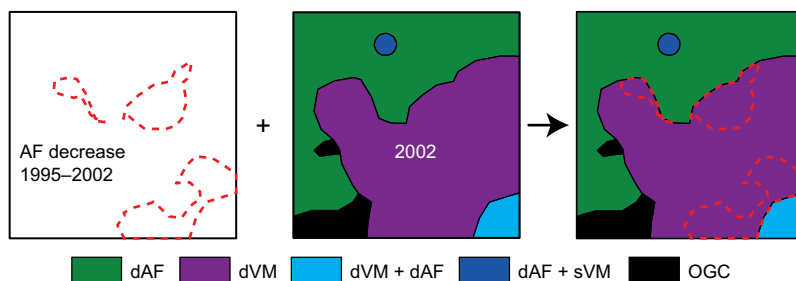
ing to each dominant vascular plant species (*A. flexuosa*, *C. villosa*, *V. myrtillus*), mosses and spruce litter patches, and summarized them for each of the study plots and years. For the dominants, cover was weighted by stand density (i.e., cover =  $1 \times$  area of the dense stand +  $0.5 \times$  area of the sparse stand). The temporal changes in cover values were analysed by Redundancy Analysis (RDA) and significance was tested by a distribution-free Monte Carlo permutation test. Spatial variability was eliminated by permuting the records of the same square within this square (technically, each square was considered to be a block and the within block permutation option was used).

Then “change polygons” for each dominant, mosses and spruce litter patches were constructed. To construct these polygons, we superimposed the appropriate maps from the beginning and the end of the study periods. The polygons thus obtained illustrated basic processes of ground vegetation dynamics, i.e., spread or retreat of the dominants, mosses and spruce litter patches and stand thinning or thickening of the dominants (Fig. 1). We also constructed polygons to represent persistence of the evaluated categories (in dominants without change in stand density). The areas of the resulting polygons were computed and summarised for each category and each plot. Simple GIS tools included in modules ArcMap and ArcTool (especially Identity, Selection and Summary Statistics) were used to perform this task (Booth and Mitchell 2001).

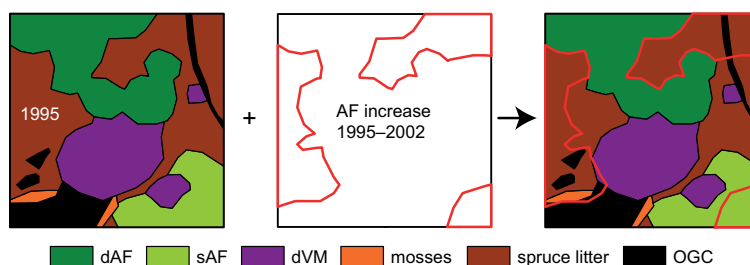
Polygons representing retreat of spruce litter (i.e., colonisation by ground vegetation or change

into another ground cover), increase of the dominants (i.e., spread or stand thickening) as well as their decrease (i.e., retreat or stand thinning) were further analysed using GIS to reveal transition trajectories for the ground vegetation dynamics. A map of the ten basic ground-cover categories and various mixed stands of the dominants, mosses and other herbaceous vegetation (e.g. mixed stand of dense *C. villosa* and sparse *A. flexuosa*, dense stand of *A. flexuosa* with mosses, mixed stand of sparse *C. villosa* and other herbaceous vegetation, etc.) was first obtained for each year (1995, 2002 and 2006) included in the study. We superimposed the five entry GIS layers (*A. flexuosa*, *C. villosa*, *V. myrtillus*, other herbaceous vegetation and the mixed layer encompassing mosses, spruce litter patches and other ground cover) using the *Union* tool. The maps of “change polygons” representing spruce litter retreat and decrease of the dominants were then overlaid with the map of ground cover from the end of the study period. We thereby identified all ground cover categories (spruce litter, other ground cover, mosses, dense and sparse stands of *A. flexuosa*, *C. villosa*, *V. myrtillus*, other herbaceous vegetation, and various mixed stands of the dominants, mosses and other herbaceous vegetation) which subsequently occurred in these polygons (Fig. 2). A similar analysis was performed for the polygons depicting increase of the dominants. However, in this analysis the map of ground cover from the beginning of the study period was used to reveal ground cover categories, which had initially occurred in these polygons (Fig. 3). The *Identity* tool was used in these steps (Booth and Mitchell 2001).





**Fig. 2.** A scheme illustrating key steps in the analysis of *Avenella flexuosa* decrease (i.e., retreat + thinning polygons). We made overlays of the polygons that depicted the decrease of this particular dominant during the study period by superimposing them on the map of ground cover from the end of this period. This analysis sought to identify the ground cover that subsequently developed in the area represented by these polygons. The figure represents one of the 1 m<sup>2</sup> plots. dAF = dense stand of *Avenella flexuosa*, dVM = dense stand of *Vaccinium myrtillus*, sVM = sparse stand of *V. myrtillus*, OGC = other ground cover.



**Fig. 3.** A scheme illustrating key steps in the analysis of *Avenella flexuosa* expansion (i.e., spread + thickening polygons). We made overlays of the polygons that depicted the expansion of this particular dominant during the study period by superimposing them on the map of ground cover from the beginning of this period. This analysis sought to identify the ground cover that initially occurred in the area represented by these polygons. The figure represents a 1 m<sup>2</sup> plot. dAF = dense stand of *Avenella flexuosa*, sAF = sparse stand of *Avenella flexuosa*, dVM = dense stand of *Vaccinium myrtillus*, OGC = other ground cover.

Changes in spruce litter patches and in the dominants in favour of other ground cover categories were measured as ratios (expressed as percentages) that reflected the areal extent of these ground cover categories relative to the total areas of the polygons depicting spruce litter retreat and decrease of the evaluated dominant. Analogously, the increase of the dominants at the expense of other ground cover categories was measured as ratios (expressed as percentages) that reflected the areal extent of these ground cover categories relative to the total areas of the polygons depicting increase of the evaluated dominant. These analyses were done separately for each 1-m<sup>2</sup> square. The resulting values were used as response variables in multivariate statistical analyses. These analyses examined differences in the transition trajectories of ground vegetation dynamics among the plots and

dependence on the initial canopy cover of spruce stands in these plots (recorded in 1996 and 2000, respectively). Only those ground cover categories that reached 10% in at least one plot were included in the statistical analyses.

Multivariate statistical analyses were performed using Canoco for Windows (ver. 4.5, Biometris — Plant Research, Wageningen, NL). A linear method of direct gradient analysis, i.e., Redundancy Analysis (RDA), or a unimodal method, i.e., Canonical Correspondence Analysis (CCA), was chosen for particular analyses (Ter Braak and Šmilauer 1998). Our choice was based on gradient lengths in the response variable data as revealed by an exploratory application of Detrended Correspondence Analysis (DCA) (Lepš and Šmilauer 2003). Significance was tested by a distribution-free Monte Carlo permutation test. The split-plot design with

whole-plots (plots) freely exchangeable and “no permutation” option at the level of split-plots (squares) was the permutation scheme applied to these analyses. In the analysis of spruce litter colonisation neither differences among the plots nor dependence on the initial canopy cover of spruce stand were statistically significant at the 5% significance level. For this reason differences among ground cover categories (replacing spruce litter patches) within the plots were analysed as well. The non-parametric Kruskal-Wallis ANOVA and a chi-square ( $\chi^2$ ) test were used in these analyses and performed by NCSS software (NCSS, Kaysville, UT, USA).

## Results

### Quantification of ground vegetation dynamics including its spatial extent

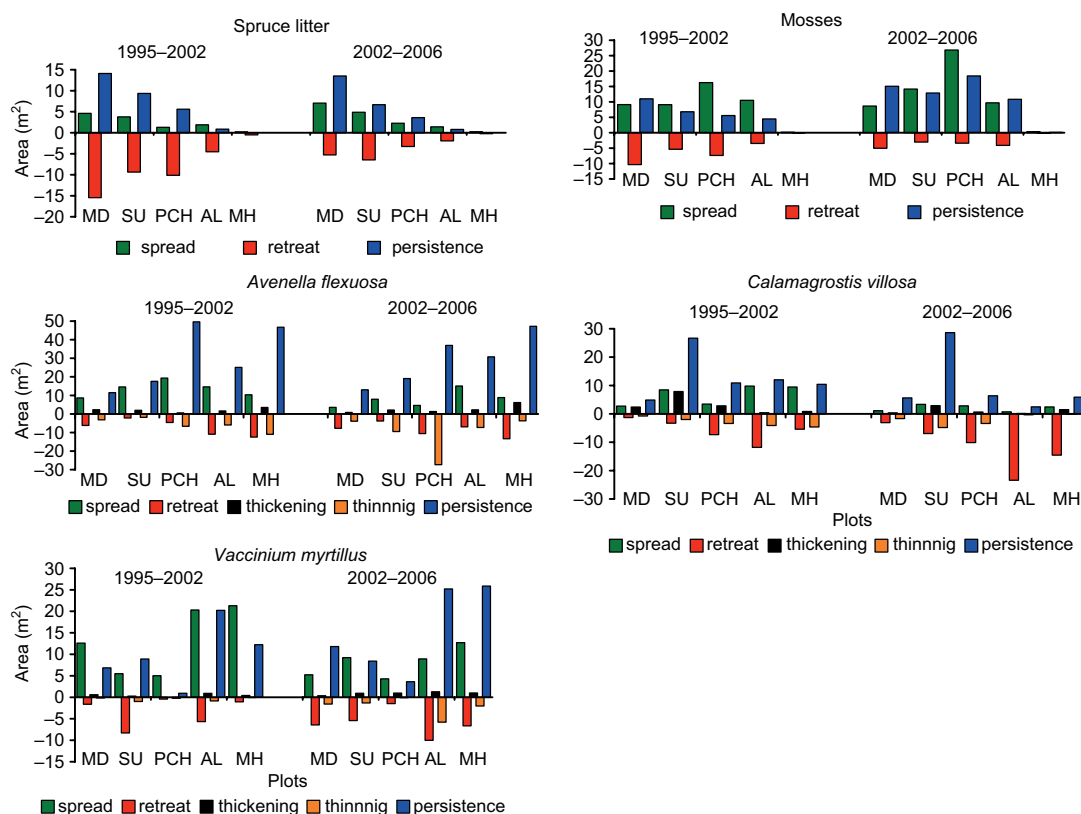
Analysis of ground vegetation dynamics revealed substantial changes in cover values of the dominants, spruce litter patches and moss layer at the spruce stands level in both study periods (RDA: Pseudo- $F = 20.50$ ,  $p = 0.002$  for the period 1995–2002 and Pseudo- $F = 4.47$ ,  $p = 0.002$  for the period 2002–2006). The general trends in ground vegetation dynamics (i.e. changes common for all plots) in the period 1995–2002 were a decrease in cover of spruce litter patches and an increase in cover of *V. myrtillus* weighted by stand density. In the second study period (2002–2006), a substantial decrease in the cover of *C.*

*villosa* weighted by stand density accompanied by an increase of moss layer cover was recorded, while the cover of spruce litter patches and *V. myrtillus* stands remained relatively constant (Table 2). For the time changes in ground vegetation typical for individual plots after removing the general trends as well as for other details see Vávrová et al. (2009).

In addition, GIS spatio-temporal analysis showed considerable fine-scale spatial dynamics in ground vegetation within the studied spruce stands, i.e., retreat from locations already occupied as well as simultaneous colonisation of new locations within the squares. Such changes in location of spruce litter patches, moss layer and ground vegetation dominants were recorded in all spruce stands regardless of the stage of their decline (Fig. 4). Representative cases include *A. flexuosa* in the Mumlavská hora, Alžbětinka and Modrý důl plots in the period 1995–2002, *C. villosa* in the Alžbětinka plot in the same period and *V. myrtillus* in the same plot in the period 2002–2006. For instance, *C. villosa* persisted in an area of 12 m<sup>2</sup> without any change in its stand density in the heavily damaged spruce stand in the Alžbětinka plot during the period 1995–2002. The same species occurred for the first time in a different area of 9.8 m<sup>2</sup>, while it retreated in a third area of 11.8 m<sup>2</sup>. Similar spatial dynamics were revealed for *A. flexuosa* in a nearly dead spruce stand in the Mumlavská hora plot in the same period (spread in to 10.3 m<sup>2</sup>, retreat in 12.5 m<sup>2</sup>) as well as for *V. myrtillus* in the less heavily damaged spruce stand in the

**Table 2.** Sum of cover values (m<sup>2</sup>) over 100 squares (1 m<sup>2</sup>) of ground vegetation dominants, spruce litter patches and the moss layer in the study plots (differing in degree of spruce stand damage) in 1995, 2002 and 2006. Plots (MD = Modrý důl, SU = Slunečné údolí, PCH = Pašerácký chodníček, AL = Alžbětinka, MH = Mumlavská hora) are arranged in order of increasing damage to their spruce stand by air pollution. At the Mumlavská hora plot, values from 60 squares (1 m<sup>2</sup>) were extrapolated to a 100 m<sup>2</sup> area for comparability with the other plots.

Plots	Spruce litter patches			Mosses			<i>Vaccinium myrtillus</i>			<i>Calamagrostis villosa</i>			<i>Avenella flexuosa</i>		
	1995	2002	2006	1995	2002	2006	1995	2002	2006	1995	2002	2006	1995	2002	2006
MD	29.6	18.7	20.6	21.3	20.1	23.7	8.6	19.2	17.0	7.1	9.1	7.0	20.7	21.6	16.0
SU	18.7	13.1	11.5	12.1	15.8	27.0	17.1	14.0	16.4	33.6	39.1	35.4	22.2	30.4	28.7
PCH	15.7	6.9	5.9	12.9	21.8	45.2	1.5	4.7	7.5	19.3	16.4	9.4	60.1	70.2	51.0
AL	5.4	2.7	2.2	7.9	14.9	20.5	26.9	41.1	36.9	18.3	14.4	2.2	41.3	42.3	45.4
MH	0.5	0.2	0.3	0.0	0.2	0.4	13.6	33.2	38.3	16.0	16.6	8.6	68.5	61.8	58.6



**Fig. 4.** Quantification of fine-scale spatial dynamics in the ground vegetation (including persistence) and changes in stand density in the dominants in the periods 1995–2002 and 2002–2006. Bars illustrate the area of the polygons ( $\text{m}^2$ ), where spruce litter patches and moss layer and the ground vegetation dominants newly occurred (spread), disappeared (retreat) or persisted (in dominants without change in stand density). For dominants, the areal extent of polygons depicting changes in stand density (thickening, thinning) are also shown. Plots (MD = Modrý důl, SU = Slunečné údolí, PCH = Pašerácký chodníček, AL = Alžbětinka, MH = Mumlavská hora) are arranged in order of increasing damage to their spruce stands by air pollution. At the Mumlavská hora plot; the values were extrapolated to a  $100 \text{ m}^2$  area for the sake of comparability with the other plots.

Modrý důl plot in the period 2002–2006 (spread to  $5.5 \text{ m}^2$ , retreat on  $8.3 \text{ m}^2$ ) (Fig. 4).

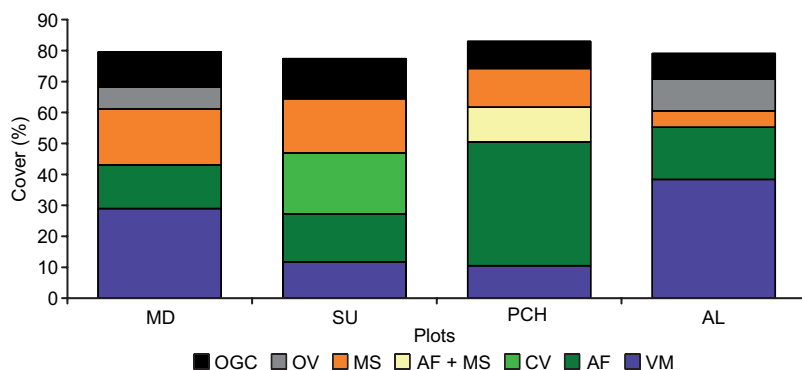
### Colonisation of spruce litter patches in 1995–2002

The differences in colonisation of spruce litter patches among the ground cover categories analysed separately within each plot were statistically significant in the Modrý důl, Pašerácký chodníček and Alžbětinka plots (Kruskal-Wallis ANOVA:  $\chi^2_{4,335} = 33.06$ ,  $p < 0.001$ ;  $\chi^2_{5,324} = 38.90$ ,  $p < 0.001$ ;  $\chi^2_{4,260} = 36.38$ ,  $p < 0.001$ ; respectively). The largest portion of polygons representing spruce litter retreat was colonised

by *V. myrtillus* in the least damaged spruce stand in the Modrý důl plot as well as in the heavily damaged stand in the Alžbětinka plot (Fig. 5). In the Pašerácký chodníček plot spruce litter patches were colonised predominantly by *A. flexuosa*. The analysis did not show significant differences in colonisation of spruce litter patches in the Slunečné údolí plot (Kruskal-Wallis ANOVA:  $\chi^2_{3,208} = 1.60$ ,  $p = 0.660$ ). The Mumlavská hora plot was not included in these analyses because its area of spruce litter patches was negligible.

Differences in the pattern of spruce litter colonisation among the four plots (CCA: Pseudo- $F = 6.13$ ,  $p = 0.092$ ) and dependence on the initial canopy cover of spruce stands (CCA: Pseudo- $F = 2.81$ ,  $p = 0.802$ ) were not significant.





**Fig. 5.** Colonisation of spruce litter patches between 1995 and 2002. The graph illustrates percentage transition of polygons depicting spruce litter retreat into different ground cover categories. The Mumlavská hora plot was not included in the graph because its area of spruce litter patches was negligible. VM = dense stand of *V. myrtillus*, AF = dense stand of *A. flexuosa*, CV = dense stand of *C. villosa*, MS = mosses, OV = other herbaceous vegetation, OGC = other ground cover; for plots see Fig. 4.

### Spatio-temporal pattern of expansion of ground vegetation dominants in 1995–2002

*Vaccinium myrtillus* spread primarily into spruce litter patches or into *A. flexuosa* stands (Fig. 6). In the least damaged spruce stand (Modrý důl plot), most polygons depicting the increase of *V. myrtillus* dominance were initially covered with spruce litter. However, in the more heavily damaged stands where a massive canopy opening had already developed by the 1980s (Alžbětinka and Mumlavská hora plots) *V. myrtillus* mainly colonised *A. flexuosa* stands or mixed stands of dense *A. flexuosa* and sparse *C. villosa*. In areas of increased *V. myrtillus*, spruce litter and *A. flexuosa* had initial covers of 44% and 17.6%, respectively, in the Modrý důl plot in comparison with 11.4% and 37.3%, respectively, in the Alžbětinka plot. The pattern of *V. myrtillus* expansion during the period 1995–2002 depended on the initial canopy cover of spruce stands (RDA: Pseudo- $F = 53.35$ ,  $p = 0.014$ , percentage of variability explained = 21.2%).

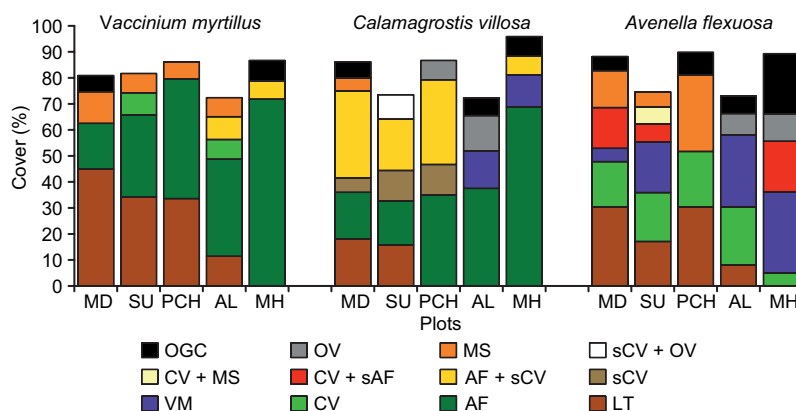
*Calamagrostis villosa* spread preferentially into locations initially occupied by *A. flexuosa* stands. Spreading of *C. villosa* was also revealed by increased stand density in locations where it had already grown in a mixed stand with *A. flexuosa*. The spruce stands with higher initial canopy cover (Modrý důl and Slunečné údolí plots) differed from the more heavily-damaged

spruce stands. They had larger proportions of spruce litter patches and sparse stands of *C. villosa* recorded in 1995 in polygons subsequently facing increase of *C. villosa* dominance between 1995 and 2002. In the heavily damaged or nearly dead spruce stands, *C. villosa* also colonised locations initially occupied by *V. myrtillus* (Fig. 6). Dependence of the pattern of *C. villosa* increase on the initial canopy cover of spruce stands was confirmed by CCA (Pseudo- $F = 5.58$ ,  $p = 0.036$ , percentage of variability explained = 6.7%).

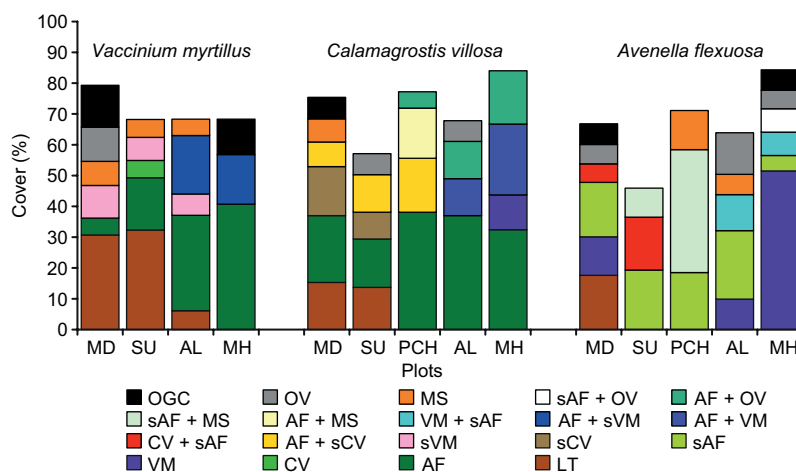
The pattern of *A. flexuosa* spreading also depended on the initial canopy cover of spruce stands in the period 1995–2002 (CCA: Pseudo- $F = 15.5$ ,  $p = 0.046$ , percentage of variability explained = 6.5%). In the less heavily damaged spruce stands, a large proportion of polygons depicting the increased dominance of *A. flexuosa* were initially covered with spruce litter or mosses. In the more damaged stands, *A. flexuosa* spread primarily into locations initially covered by *V. myrtillus* (Fig. 6).

### Spatio-temporal pattern of decrease in ground vegetation dominants in 2002–2006

In the spruce stands with higher initial canopy cover (slightly damaged forest stands), the large proportion of polygons representing the decline



**Fig. 6.** Differences among plots in ground cover categories initially occurring in the locations colonised by ground vegetation dominants between 1995 and 2002. The graph shows ratios of the area of ground cover categories (expressed as percentages) of polygons representing increase of the particular dominant. LT = spruce litter, sAF = sparse stand of *A. flexuosa*, sCV = sparse stand of *C. villosa*; for other ground cover categories and plots see Figs. 4 and 5.



**Fig. 7.** Differences among plots in ground cover categories subsequently occurring in polygons for which a decline of ground vegetation dominants was recorded between 2002 and 2006. The graph shows ratios of the areal extent of ground cover categories expressed as percentages of polygons representing the decline of a particular dominant. The Pašerácký chodníček plot was not included in the analysis of *V. myrtillus* decrease because the area of polygons representing this change was negligible. sVM = sparse stand of *V. myrtillus*; for other ground cover categories and plots see Figs. 4, 5 and 6.

of *C. villosa* changed to (1) spruce litter patches and (2) sparse stands of *C. villosa* between 2002 and 2006 (Fig. 7). In the heavily damaged or nearly dead spruce stands, *C. villosa* was replaced mainly by *A. flexuosa* and/or *V. myrtillus* (Fig. 7). Dependence of differences in the pattern of *C. villosa* decline among the plots on the initial canopy cover of spruce stands was confirmed by CCA (Pseudo- $F = 7.25$ ,  $p = 0.014$ , percentage of variability explained = 7.6%).

The largest proportion of polygons representing the decline of *A. flexuosa* changed to: (1) sparse stands, (2) sparse stands with mosses or (3) *V. myrtillus* stands. Spruce litter patches replaced *A. flexuosa* stands only in the Modrý důl plot. The decline of *A. flexuosa* resulting in its replacement by *V. myrtillus* was recorded predominantly in the Mumlavská hora plot. CCA confirmed differences in the pattern of *A. flexuosa* decline among the plots (Pseudo- $F = 11.25$ ,

$p = 0.014$ , percentage of variability explained = 20.9%). However, dependence on the initial canopy cover of spruce stands was not confirmed at the 5% significance level ( $p = 0.228$ ).

In less heavily damaged spruce stands in the Modrý důl and Slunečné údolí plots, *V. myrtillus* was replaced mainly by spruce litter patches or its decline resulted from reduction of its canopy density to that of sparse stands. At Modrý důl, 30.7% of the polygons depicting the decline of *V. myrtillus* between 2002 and 2006 changed to spruce litter patches and 10.6% of these polygons changed to sparse stands of *V. myrtillus*. The decline of *V. myrtillus* resulting in replacement of this dominant by *A. flexuosa* was apparent in the Alžbětinka and Mumlavská hora plots. The highest percentage of polygons representing *V. myrtillus* decline showed subsequent cover by *A. flexuosa* or by mixed stands of *A. flexuosa* with sparse *V. myrtillus* in these heavily damaged or nearly dead spruce stands (Fig. 7). Dependence of the spatio-temporal pattern of *V. myrtillus* decline in 2002–2006 on the initial canopy cover of spruce stands was confirmed by RDA (Pseudo- $F = 20.3$ ,  $p = 0.046$ , percentage of variability explained = 13.9%).

## Discussion

### Fine-scale spatial dynamics in ground vegetation within the damaged spruce stands

Our study detected (i) substantial changes in cover values of the vascular plant species dominant in the ground vegetation, moss layer and spruce litter patches in spruce stands damaged by air pollution (Vacek *et al.* 1999, Vacek *et al.* 2007, Vacek *et al.* 2013) as well as (ii) considerable fine-scale spatial dynamics in ground vegetation within these stands, i.e., retreat from locations already occupied and accompanied by simultaneous colonisation of new locations within the stands. Such changes in the location of ground vegetation dominants were recorded in all spruce stands studied, regardless of the stage of decline. The ground layer of mountain spruce stands damaged by air pollution represents a mosaic of patches differing in canopy cover, time

after canopy opening and microhabitat conditions, e.g. microrelief, soil type, and water conditions. These patches also differ necessarily in ground vegetation dynamics. Different and even opposing processes of ground vegetation dynamics can thus occur simultaneously within partly damaged and gradually declining forest stands. Processes under less defoliated spruce crowns can differ from those occurring in newly formed canopy gaps as well as from processes occurring in old gaps. This fine-scale mosaic of patches distinguishes the ground layer and its dynamics in forests damaged by air pollution from that occurring in areas affected by large-scale severe wind disturbances or insect outbreaks accompanied by a sudden total decline of the tree layer (e.g., Fischer *et al.* 2002, Wohlgemuth *et al.* 2002, Jonášová and Prach 2008, Lain *et al.* 2008).

The fine-scale spatial dynamics in ground vegetation revealed by our results can influence the natural regeneration of Norway spruce in mountain ecosystems affected by air pollution. Many previous studies have pointed out that sufficient availability of suitable microhabitats is important for the occurrence of Norway spruce seedlings in mountain and boreal spruce forests (Ohlson and Zackrisson 1992, Hörnberg *et al.* 1997, Jonášová and Prach 2004, Hunziker and Brang 2005, Kupferschmid and Bugmann 2005). The dominants, mosses, spruce litter patches and other ground cover categories treated in this study are known to differ in the extent to which they favour Norway spruce regeneration (e.g., Jäderlund *et al.* 1997, Hanssen 2003, Jonášová and Prach 2004, Kupferschmid and Bugmann 2005, Vacek *et al.* 2013). Their marked changes of location and their mutual transitions can therefore contribute to higher seedling mortality and can also limit spruce regeneration by restricting the availability of suitable microhabitats. In our plots, spruce litter patches and mosses have been shown to provide more favourable conditions for natural regeneration of Norway spruce compared with the ground vegetation dominants (Vávrová *et al.* 2007). Therefore, the probability of spruce seedling mortality in spruce litter patches or in mosses increased considerably after the colonisation of these microhabitats by the ground vegetation dominants. Moreover, the favourableness of the dominants for spruce seedling

survival decreased in the following order: *V. myrtillus* > *A. flexuosa* > *C. villosa* (Vávrová *et al.* 2007). Consequently, lower number of seedlings survived in patches where *V. myrtillus* stand had been replaced by the grasses. At other locations the opposite change in ground vegetation took place simultaneously, e.g. the dominant can decline being replaced by mosses, and the favourableness of these locations for Norway spruce seedling germination increased. However, the process of natural regeneration is probably hampered by the relatively quick plant dominants changes. The limitation of spruce natural regeneration due to the low availability of suitable microhabitats may alter the internal dynamics and subsequent development of these valuable forest ecosystems (Vacek *et al.* 1999).

Comparison of the applied GIS spatio-temporal analysis based on quantification of the areal extent of the “change polygons” with the results of the conventional method, comparing vegetation dominant cover values at the beginning and the end of observation, showed that the conventional method failed to reveal the real extent of ground vegetation dynamics in partly disturbed and gradually regenerating forest stands. Lack of change in cover values of the evaluated species or other ground cover categories does not necessarily imply a lack of ground vegetation dynamics. Changes may occur in such a way that locations of species or categories change between time one and time two, while the cover values (or quantities) remain the same. A similar approach has been applied to analyses of land-cover transitions in landscape ecology (e.g., Pontius *et al.* 2004, Braimoh 2006). Methods of this sort offer greatly improved insights into processes that potentially determine patterns of vegetation dynamics (Pontius *et al.* 2004).

### **Successive pattern of ground vegetation dynamics in mountain Norway spruce ecosystems damaged by SO<sub>2</sub> air pollution**

We compared both the extent of changes in cover values of the spruce litter patches, moss layer and ground vegetation dominants, and the transition trajectories of these changes among the plots differing in canopy cover of spruce stands at the

beginning of our study. From these two variables and from the time since canopy opening and the subsequent dynamics of spruce stands during the study periods, we deduced the following successive patterns of ground vegetation dynamics in mountain Norway spruce ecosystems damaged by air pollution.

The area of spruce litter patches (*see* Table 2) corresponded to the canopy cover of the respective spruce stands (*see* Table 1). During tree layer decline these patches were colonised by ground vegetation and gradually diminished in size. The increase of ground vegetation cover in response to tree layer damage and the decrease in canopy cover agrees with the results of studies on the influence of insect outbreaks or storm events on forest ecosystems (e.g., Wohlgemuth *et al.* 2002, Jonášová and Prach 2008, Lain *et al.* 2008). The pattern of spruce litter colonisation in our study seemed to depend on the course of spruce stand decline and the rate of canopy cover opening. The results indicate that *V. myrtillus* occupied spruce litter patches primarily in stands that were slightly declining. In the stands where canopy cover decreased substantially, the bulk of spruce litter patches was colonised by grasses, especially *A. flexuosa*. The expansion of *C. villosa* was probably more dependent on favourable soil conditions (Vávrová *et al.* 2009), especially sufficient soil moisture content (van Roon 1993). Similar results concerning the dynamics of *V. myrtillus* patches in relation to the occurrence of canopy gaps were obtained by Maubon *et al.* (1995) in mountain spruce forests in France, affected by storm disturbance. They showed that gap size, together with the presence or absence of *V. myrtillus* prior to the death of the trees, could determine whether an ericaceous or herbaceous vegetation would invade these openings. Small gaps between the trees were invaded by dense *V. myrtillus* stands whereas larger gaps were colonized by herbaceous vegetation.

*Calamagrostis villosa* stands seemed more likely to expand into sites already occupied by *A. flexuosa*. The ability of *C. villosa* to thrive in declining forest stands might be related to its facultative dependence on mycorrhizal hyphal links to *A. flexuosa* (Vosatka and Dodd 1998, Malcová *et al.* 1999). *C. villosa* could become a more aggressive competitor due to the contri-

bution of mycorrhizal fungi to nutrient acquisition (Vosatka and Dodd 1998) and replace *A. flexuosa* at sites with a higher irradiance on the forest floor below a reduced canopy. Similarly, Pyšek (1992), who studied the dominant species exchange during succession in areas reclaimed after acid rain deforestation, found that *C. villosa* invaded into *A. flexuosa* stands. Decreased *A. flexuosa* cover, probably due to competition with *C. villosa*, was recorded also under the completely dead canopy of mountain spruce forests affected by bark beetle outbreak (Jonášová and Prach 2008). Somewhat different results were obtained by Bauer (2002), who found decreased cover of *A. flexuosa*, but no change in that of *C. villosa*, three years after bark beetle outbreak in spruce forests of the Bavarian Forest Mts. (Bayerischer Wald, Germany).

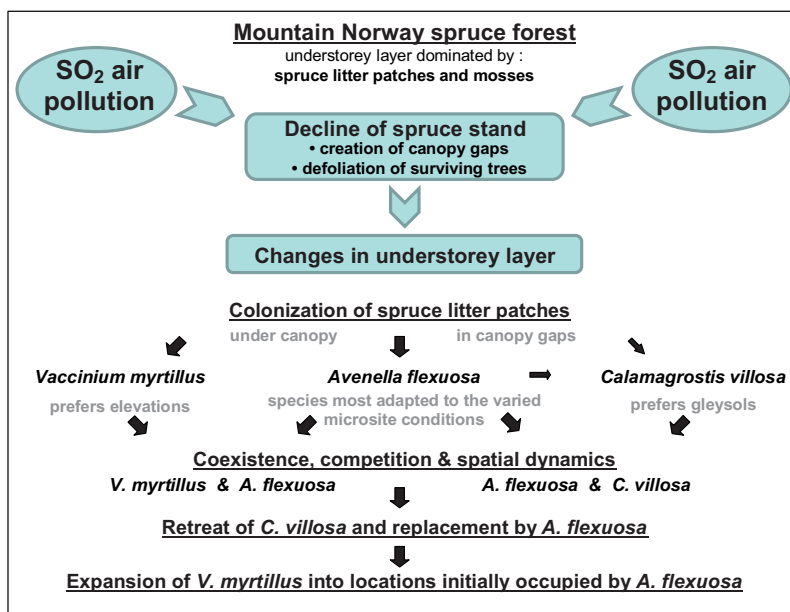
The opposite process, i.e., a considerable retreat of *C. villosa* and its replacement by *A. flexuosa*, was particularly evident at plots where massive canopy opening of spruce stands had already occurred in the 1980s. This result suggests that *C. villosa* first began to retreat after a period of coexistence and mutual competition between the grasses. This is consistent with successional trends in ground vegetation, recorded by van Roon (1993) in clearings after the dieback of the Giant Mts. spruce forests. Soukupová et al. (1998) showed that on podzols the life cycle of *C. villosa* lasted about seven or eight years; then was replaced by *A. flexuosa*. We assume that higher solar irradiance at the forest floor accelerated the decomposition and mineralisation of accumulated organic matter. These processes led to limitation of *C. villosa* by low organic matter content in the soil (Pyšek 1994, Kooijman et al. 2000) and to its gradual replacement by *A. flexuosa* after several years. Mineralisation can also be enhanced by reduced soil moisture and by a different chemical composition of dead plant biomass, consisting primarily of grass litter characterised by a lower C/N ratio and lower lignin content in comparison with the formerly dominant spruce and dwarf shrub litter (Żołnierz et al. 2000). The influence of the studied dominant species (e.g. *V. myrtillus* and *A. flexuosa*) on the variations in quality of humic substances was confirmed on our research plots by Bonifacio et al. (2008).

*Vaccinium myrtillus* colonised *A. flexuosa* stands shortly after the retreat of *C. villosa*. Potential causes of this change may have included a decrease in the thickness of the F-layer of the soil organic profile (van Roon 1993) or a shortage of certain nutrients or elements essential for *A. flexuosa* growth, after long-term occupancy of particular locations by this species. The remarkable spatial dynamics of *A. flexuosa* within the plots, recorded in all stands during both study periods, seems to support this argument. Pyšek (1994) noted that the occurrence of *A. flexuosa* was positively correlated with potassium content in the soil. The higher susceptibility of *A. flexuosa* than *V. myrtillus* to drought might be a possible contributing factor. *A. flexuosa* has rhizomes in the upper part of the humus layer (Schimmel and Granstrom 1996), whereas *V. myrtillus* rhizomes penetrate deeper, namely into the upper part of the mineral soil (Rydgren et al. 1998).

The final expansion of *V. myrtillus* into sites formerly occupied by the grasses could generally indicate the beginning of recovery of the ground vegetation to a composition more similar to that recorded in old-growth mountain Norway spruce forests before the period of air pollution, with a dominance of dwarf shrubs over grasses (Matuszkiewicz and Matuszkiewicz 1969). Żołnierz et al. (2000) observed an analogous increase in cover of dwarf shrubs at the expense of grasses in the Giant Mts. in areas with spruce stands regenerating after deforestation.

We compared the extent and transition trajectories of changes in ground vegetation among our plots differing in the initial canopy cover of the spruce stand, its subsequent dynamics and time since canopy opening. From this, we deduced the successive patterns of ground vegetation dynamics during and after the period of forest decline in our research plots located in mountain Norway spruce forests damaged by SO<sub>2</sub> air pollution and other contributing stress factors (Fig. 8). Preferences of the ground vegetation dominants for specific microhabitat conditions included in this scheme were studied and discussed in our previous paper (Vávrová et al. 2009). Based on the study of available literature concerning this topic (e.g., van Roon 1993, Pyšek 1994, Vacek et al. 1999, Kooijman

**Fig. 8.** A scheme illustrating the successive pattern of ground vegetation dynamics in our five plots in mountain Norway spruce stands damaged by air pollution.



*et al.* 2000, Żołniercz *et al.* 2000) we consider the increased amount of solar irradiance of the ground layer below canopy openings and subsequent changes of soil characteristics (especially in organic soil layers) to be factors or processes releasing and driving the recorded changes in ground vegetation.

The ground vegetation dynamics in forests damaged by SO<sub>2</sub> air pollution shown in our study differ from the dynamics observed in natural forest cycles (Dittrich *et al.* 2013). They investigated the influence of stand age-related shifts in forest structure, and related changes in solar irradiance and soil conditions on the diversity and composition of ground vegetation in a high-mountain old-growth Norway spruce forest in Germany. In all five developmental stages of the natural forest, the dynamics of the herb layer was strongly dominated by *A. flexuosa*, *C. villosa*, *Galium saxatile* and *V. myrtillus*. In contrast to our study, the mean cover values did not significantly change (Dittrich *et al.* 2013). Similarly, Kirchner *et al.* (2011) did not observe any pronounced changes in the vegetation composition or diversity in response to forest gap dynamics in near-natural spruce forests. Nevertheless, the cover of some frequent herb layer species, including *C. villosa* and *V. myrtillus*, was found to change with gap age (Kirchner *et al.* 2011).

The shoot densities of *V. myrtillus* were highest at an intermediate gap age (15–60 years) and *C. villosa* had its highest densities in the oldest gaps (> 60 years), which contrasts with the strong retreat of *C. villosa* observed in our plots after the period of its expansion, and the subsequent expansion of *V. myrtillus* into plots formerly occupied by the grasses (Fig. 8).

### Changes characteristic of recovery of ground vegetation in less damaged spruce stands

For the period 2002–2006, the results of GIS analyses of the transition trajectories of changes in ground vegetation indicated that all dominants partially retreated in the absence of competition from other ground vegetation in the less damaged spruce stands. Either the dominant stands became sparser or they disappeared completely and were replaced by spruce litter patches. Higher initial spruce canopy cover was associated with this pattern of retreat of the dominants. We assume that the early stages of recovery of surviving trees could be the cause of such retreats. More intensive growth of secondary shoots (Polák *et al.* 2007) could result in less solar radiation penetrating through the canopy,



providing less favourable conditions for growth of the ground vegetation dominants.

## Conclusions

Our results suggest the following successive pattern of ground vegetation dynamics after canopy opening in mountain Norway spruce forests damaged by air pollution. Spruce litter patches diminished, being colonised predominantly by *V. myrtillus* under the gradually defoliating tree crowns, and by the dominant grasses, *A. flexuosa* and *C. villosa* in canopy gaps. *C. villosa* often spread into sites already occupied by *A. flexuosa*. After several years of coexistence and of dynamic spatial interactions among the dominant grasses within the stands, *C. villosa* first began to retreat being replaced by *A. flexuosa*. Then the second wave of *V. myrtillus* expansion occurred. This species spread into sites formerly occupied by *A. flexuosa* stands. These changes could generally indicate beginning recovery of the ground vegetation to a species composition more similar to the composition recorded in old-growth mountain Norway spruce forests before the period of air pollution, with a dominance of dwarf shrubs over grasses.

The less damaged spruce stands differed from the more severely impacted ones in the more distinct retreat of all dominants during reduced competition with other ground vegetation recorded in the second study period. This retreat was probably a consequence of the partial recovery of the surviving trees.

The considerable fine-scale spatial dynamics in ground vegetation within the damaged spruce stands implies that the ground layer of these ecosystems represents a mosaic of patches differing in canopy cover, time since canopy opening, microhabitat conditions and necessarily also in processes occurring in the ground vegetation. Spruce litter patches, mosses and the ground vegetation dominants treated in this study are known to differ in their favourableness for Norway spruce regeneration. Their changes of location and mutual transitions, detected by the applied GIS analyses of vegetation micro-maps data, can therefore contribute to higher spruce seedling mortality and affect the further development of these valuable ecosystems.

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